Note

Alternative Reproductive Tactics in Context: How Demography, Ecology, and Behavior Affect Male Mating Success

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abstract: Exploitation of sexual signals by predators or parasites increases costs to signalers, creating opportunities for establishment of alternative reproductive tactics (ARTs). In field crickets, males calling may attract acoustically orienting parasitoid flies. Alternatively, males behaving as satellites forgo calling and attempt to intercept females attracted to callers. We modeled the contribution of calling versus satellite behavior to male reproductive success in the larger context of variation in ecology (parasitism rate, background mortality), demography (density, sex ratio), and female behavior (phonotaxis, mating choosiness). Male mating success was most influenced by number of females (standardized effect size 0.42), followed by female choosiness (0.33), background mortality (−0.31), number of males (−0.28), and parasitism rate (−0.21). The smallest effects were phonotaxis (0.10) and satellite behavior (−0.09). Although satellite behavior ameliorated negative effects of parasitism, its comparative effect was slight. ARTs seem most likely to evolve and persist when a single selection pressure on signaling is particularly strong.

Keywords: alternative reproductive tactics, ecological context, field crickets, individual-based simulation, parasitoids, satellite behavior.

Introduction

Alternative reproductive tactics (ARTs) are two or more distinct behavioral and/or morphological traits that represent alternate ways of achieving reproductive success (Oliveira et al. 2008). Alternative tactics evolve in the context of intrasexual competition, arising when different tactics yield differential reproductive success. An alternative trait may be fixed for an individual's life, or the same individual may pursue different tactics through time, alternating among them on timescales ranging from seconds to most of a lifetime. Typical research questions involving ARTs usually examine the relative fitnesses of alternative phenotypes—for example, what favors fixed versus flexible alternatives, what conditions influence switching between alternate tactics (i.e., the nature and mechanism of decision rules), or what controls the relative frequencies of alternative tactics in a population (Shuster and Wade 2003; Taborsky et al. 2008). However, because expression of ARTs occurs within a broader context established by ecological conditions and population demographics, this context can serve as a filter that determines which individuals actually arrive at the point where a tactic is expressed. Our objective here is to examine variation in alternative mating tactics in a larger ecological, demographic, and behavioral context and use a simulation experiment to assess the relative contribution of each of these components to variation in individual fitness.

A common type of ART involves differing expressions of a sexual signal (Brockmann and Taborsky 2008). Under sexual selection, an attractive signal often evolves to become more costly to its possessor (usually male) and more conspicuous to the intended receiver (usually female; Andersson 1994). However, as a signal's cost rises, its possessor becomes increasingly vulnerable to exploitation by an individual that employs an alternate tactic that does not rely on the signal (Taborsky 1998). As a signal becomes more conspicuous, it becomes vulnerable to eavesdropping by unintended recipients (Zuk and Kolluru 1998; Peake 2005). Eavesdroppers, which may be of the same or different species from the signaler, may also exploit the signal to their own benefit, often adding further to the signal's cost to the original signaler. In both cases, increasing costs to the signaler leads to a greater opportunity for establishment of an alternative tactic (Gonçalves et al. 2008).

A well-studied example of eavesdropping influencing alternative mating tactics occurs in field crickets (Orthoptera: Gryllidae). In field crickets, males produce a conspicuous call to attract females. However, in some species this call also attracts parasitoid flies, with potentially deadly consequences for the male (Cade 1975; Walker and Wineriter 1991). Female

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flies (Diptera: Tachinidae, Ormiini) home in on a calling male and deposit free-living larvae on or around him. Larvae burrow into a male and begin consuming his tissues (Adamo et al. 1995). Males remain active (and continue to call) immediately after the initial infestation but cease calling after a few days (Cade 1984; Kolluru et al. 2002). After about a week, larvae emerge to pupate, and the male cricket dies. The increased cost of calling due to acoustically orienting parasitoid flies creates an opportunity for the emergence of an alternative tactic, satellite behavior, where noncalling males (satellites) attempt to intercept females attracted to callers (Cade 1975, 1980). Males behaving as satellites are often phonotactic as well, approaching and settling near calling males. Males may alternate between behaving as a caller or satellite on timescales ranging from minutes to hours to nights. The fitness trade-offs are straightforward: satellite behavior increases a male's longevity by substantially reducing his probability of becoming parasitized, but noncalling males experience substantially reduced female encounter rates compared to callers.

Following on the work of Cade and his colleagues as well as our earlier analysis (Rowell and Cade 1993; Walker and Cade 2003; Rotenberry et al. 2015), we used the field cricket system to answer questions about the influence of demographic, environmental, and behavioral scenarios on mating success. Unlike earlier studies, ours treated satellite behavior as a continuous trait: a male called or behaved as a satellite each night with some probability. Such a scenario is more realistic for many animals than an all-or-none strategy. We then asked what propensity to behave as a satellite on any given night maximized a male's reproductive success under different conditions, including variation in density, sex ratio, parasitism rate, background mortality rate, female phonotaxis, and female mate acceptance. We observed that even modest parasitoid pressure could select for a pure satellite strategy (i.e., behave as a noncalling satellite every night). Indeed, although we applied a continuous selection gradient (intensity of parasitization) to a continuous character trait (propensity for satellite behavior), under many conditions we observed a discontinuous outcome—one or the other end of the behavioral axis (mostly satellite vs. mostly caller) was favored, rarely intermediates. However, we also observed that a mixed strategy (at least some nights calling) could persist even under high parasitism risk under certain conditions: high background mortality (i.e., mortality independent of parasitism), low population density, a highly female-biased sex ratio, high female phonotaxis (a female's willingness to approach a calling male she detected), and high female choosiness (a low propensity to mate with a male she encountered). We concluded that the substantial variation in these attributes that normally occurs in natural populations renders it unlikely that parasitoid pressure alone would yield fixation of pure satellite behavior (i.e., the loss of calling; Rotenberry et al. 2015).

In this earlier work, we varied each of the independent variables over a wide range. Moreover, we did so holding each of the other independent variables at a constant value, and we examined the effects of each independent variable separately from the others. As our focus was on factors influencing the relative fitness of alternative tactics, this approach was sensible. In reality, however, these independent variables act in concert. Here we ask, what is the relative weight or contribution of each of these ecological and behavioral variables to overall fitness when considered simultaneously? For example, is the benefit of behaving as a satellite versus calling outweighed by the effect of population density or sex ratio? We now seek to place the relative importance of variation in ARTs in the context of other features that influence male reproductive success. To do so, we revisit our original model, only now we vary the independent variables (including parasitism rates and propensity for satellite behavior) in a fully crossed factorial design. This, in turn, will help us to understand the broader circumstances likely to lead to the evolution of ARTs and evaluate the relative strength of different drivers of ARTs in other animals.

Methods

Modeling Behavior

Our model, which extends those previously articulated by Cade and colleagues (Rowell and Cade 1993; Walker and Cade 2003), has been described in considerable detail elsewhere (Rotenberry et al. 2015); what follows is a brief summary of its salient features. We used the agent-based, spatially explicit simulation modeling environment made available in NetLogo (Wilensky 1999). Each individual occupies a patch in a landscape (a 50 × 50 grid) and moves among patches and interacts with other crickets according to particular rules. These movements and interactions take over 240 discrete time steps throughout a night. A step is equivalent to 3 min in a 12-h night, and a patch is functionally equivalent to a 1 × 1-m square. A moving cricket can traverse one square per time step.

Rules governing movement and behavior are simple. At the start of each night, a male decides (with some probability) whether to call or to behave as a satellite. Males behaving as callers remain stationary and are detectable by females over a particular radius. While calling, a male has a particular risk of being parasitized. If parasitized, he continues to follow male behavioral rules for three nights and then dies. Males behaving as satellites do not call and thus do not attract females from a distance. A satellite is phonotactic toward callers and settles near any he encounters. Satellites are not parasitized. Both callers and satellites can mate with an encountered female. Females are phonotactic, at-

tracted (with some probability) to move toward a calling male she detects, but she may encounter satellites as well. She mates with whomever she encounters with some particular probability (equal for callers and satellites). If she decides not to mate with an encountered male, she moves on. The probability of attraction toward a calling male and the probability of mating with whom she encounters are independent elements of female choosiness. When not settled or moving toward a calling male, both satellites and females wander randomly. An encounter occurs whenever a female moves into a patch adjacent to one occupied by a male; males, however, do not occupy adjacent patches. In all simulations reported here, we fixed male and female auditory radii (number of patches over which a calling male could be detected) at 20.

At the end of a night, the demographic consequences are reckoned. The lifetime number of opposite-sex encounters and the number of matings are updated for each individual. A male that spent the night as a caller is parasitized with a certain probability, and males parasitized three nights previously are removed from the population (i.e., die). Individual crickets die with a probability based on a nightly death rate independent of parasitism, and all survivors age one night. To maintain density and sex ratio throughout a run, dead individuals are replaced in kind. Nights then repeat until the last male of the original cohort dies, after which the simulation run ends. The principal statistic we collect at the end of a run is the number of females mated during a male's lifetime averaged over all males in the initial cohort, plus males' average age at death. We use data only from males in the initial cohort, as these are all individuals who have lived a complete life; many noncohort males have not yet died and thus would yield biased lifetime data. To account for the stochastic nature of sex and death, we performed 10 runs for each combination of input variables.

Modeling Relationships among Variables

Our previous simulations (Rotenberry et al. 2015), as well as those of Walker and Cade (2003), yielded very high correlations (on the order of $r > 0.97$) between age at death (life span) and the number of females encountered, as well as between the number of females encountered and the number of females mated. These correlations form the core of a model that describes how the variables and behaviors noted above directly and indirectly influence male fitness as measured by the number of females he mates with during his lifetime (fig. 1). For example, in the absence of parasitoids, life span is directly influenced by the background mortality rate. Life span is also affected by parasitism rates, but the effect is moderated by the degree of satellite behavior males express. Although longer-lived males on average encounter more females, encounter rates are modified by other variables. Density and sex ratio interact to produce the absolute number of males and number of females in a simulated population; as the number of females rises, the opportunities for encounters increases, whereas more males leads to more competition for females and more interference in their potential acquisition. With respect to encounter rates, satellite behavior has a negative effect, as females cannot be attracted to a male that does not call. Similarly, a female's propensity to move toward a male she does detect at a distance (phonotaxis probability) influences encounter rates. Finally, once a male does encounter a female, variation in female choosiness (mating probability) determines whether

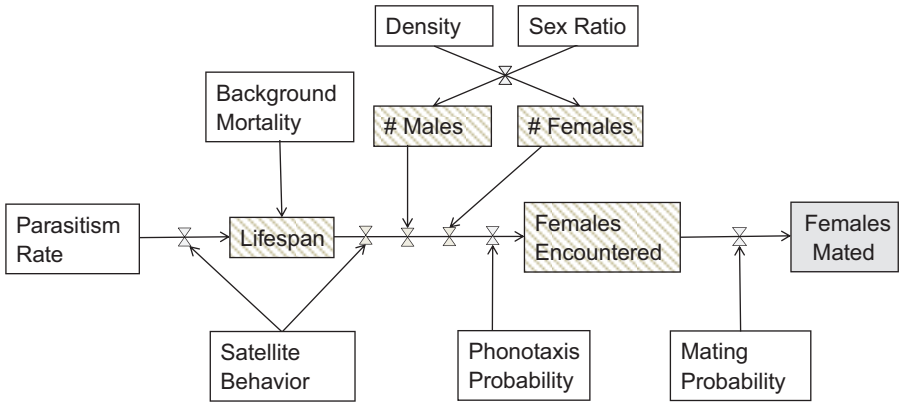

Figure 1: Relationships among variables influencing cricket male fitness (number of females mated) in a caller-satellite-parasitoid system. Open boxes denote independent exogenous variables, hatched boxes denote endogenous latent variables, and the filled box denotes the dependent variable.

she actually mates with him. The question we now wish to address is, how, in this broader context of variation in ecological (background mortality, parasitism rate), demographic (density, sex ratio), and female behavioral (phonotaxis, mating probability) traits, does variation in the expression of alternative reproductive tactics (calling vs. satellite) contribute to male fitness?

The Simulations

We parameterized our simulations based on our own field investigations of *Teleogryllus oceanicus* in the Hawaiian Islands, where it is parasitized by *Ormia ochracea* (Zuk et al. 1993; Simmons and Zuk 1994; Kolluru 1999; M. Zuk, J. Rotenberry, and R. Tinghitella, unpublished data), as well as values used by Walker and Cade (2003) based on extensive studies of *Gryllus texensis*, also parasitized by *O. ochracea*. We used four values for each of our seven independent variables, chosen to span the range of values for each that we used in our previous simulations (table 1; Rotenberry et al. 2015). Our fully crossed design generated 16,386 unique combinations of variable values, each of which was run 10 times.

The Analysis

We used structural equation modeling (SEM; Bollen 1989) to analyze the contributions of the independent variables (table 1) to variation in male fitness as indexed by the lifetime number of females with whom he mated. Explicitly multivariate, SEM links together variables in a system of simultaneous regression equations. Exogenous variables are analogous to independent variables in regression, whose values and variance are determined independently of all others, whereas endogenous (dependent) variables are those whose values and variance are determined by other variables in the model. Endogenous variables may also serve as input variables for other relationships within a model (e.g., life span in fig. 1). Structural equation modeling is theory oriented in that links (paths) are directed, implying specific cause-effect relationships. Standardized path coefficients are like partial regression coefficients, with the expected impact of a change in one variable on another (in our case, number of females mated) controlling for the direct and indirect effects of all the other variables (Grace and Bollan 2005). Thus, path coefficients yield the relative importance of different paths or processes in explaining change in a dependent variable. Path coefficients do not represent a partitioning of variance (i.e., a partial R^2), although SEM does provide an overall goodness-of-fit index analogous to an R^2 in regression. An additional measure of fit of an SEM to data is the root mean square error of approximation (RMSEA; Browne and Cudeck 1993). A fit is assessed as "excellent" when RMSEA < 0.05 and "good" when RMSEA > 0.08, although there is little empirical support for the use of these or similar cutoff values in determining the adequacy of a model fit (Chen et al. 2008). As with all simulated data, standard inferential statistical tests are not appropriate (White et al. 2014).

We applied SEM to the paths represented in figure 1 with one change: we substituted number of males and number of females, both of which are a direct function of density and sex ratio, for density and sex ratio. This is because the effects of density and sex ratio are directly manifest through the number of available females and the number of competing males, yielding a more relevant interpretation of path coefficients. We treated age and number of females encountered as endogenous variables (hatched boxes in fig. 1) and the seven independent variables as exogenous (open boxes in fig. 1). We created three latent variables (related to the bow tie symbols on the paths in fig. 1): (1) an interaction between females encountered and probability of mating, to affect females mated; (2) encounter rate, to mediate between age, number of males, number of females, probability of satellite behavior, phonotaxis, and females encountered; and (3) an interaction between probability of satellite behavior and parasitism rate, to affect life span. The latter interaction allowed us to set the direct path from satellite behavior to age to 0; satellite behavior influences life span only in the presence of parasitoids. We also partitioned the data into four subsets based on the four values of parasitism rates and analyzed each separately.

Table 1: Parameter values used for simulations

Ecology		Male behavior	Demography		Female behavior	
Parasitism (prob. parasitism if singing)	Mortality (nightly prob. death)	Satellite (nightly prob.)	Density (total no. crickets)	Sex ratio (% female)	Phonotaxis (prob. to approach caller)	Mating (prob. on encounter)
0	.02	0	25	50	.3	.3
.1	.04	.33	50	60	.5	.5
.2	.06	.67	75	70	.7	.7
.3	.08	1	100	80	.9	.9

Note: Each value for each variable was used in combination with every other variable value. Prob. = probability.

We implemented SEM using PROC CALIS in SAS 9.3 (SAS Institute 2010), which uses maximum likelihood to solve for path coefficients. Results are reported as standardized path coefficients for the total effect of each exogenous variable on the lifetime number of females mated.

Results

As expected, increasing background mortality, parasitism rate, and number of males decreased the lifetime number of females mated, whereas increasing the number of females in the population as well as their phonotaxis probability and mating probability had positive effects (table 2). As an effect of our very large sample size, standard errors of path coefficients (not shown) were on the order of 0.0010–0.0017. The goodness-of-fit index for the overall model was 0.9866, and RMSEA = 0.0529.

Overall, the largest effect on a male's mating success (i.e., lifetime number of females mated) was associated with the number of females, followed by mating probability, background mortality, and number of males (table 2). The smallest effects were due to phonotaxis probability and variation in propensity for satellite behavior, with parasitism rate intermediate. Data underlying table 2 are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.kh654 (Rotenberry and Zuk 2016).

The magnitude of effects changed for some variables with changes in parasitism rate (table 2). Notably, in the absence of parasitoids, increasing probability of satellite behavior had a strong negative effect, and as the sole source of mortality, the path coefficient of nightly mortality rate increased in absolute value substantially (negative). The largest change in path coefficients occurred in the transition from no parasitism to some parasitism, with the largest absolute changes in the effects of nightly mortality and probability of satellite behavior, with each becoming less negative. As parasitism rate increased further, there was relatively little change in path coefficients, except that satellite behavior began to have a positive contribution to reproductive success.

Discussion

To fully understand the evolutionary implications of variation in a trait, it is important to see that variation expressed in the larger context of the range of environmental circumstances in which it may occur. Doing so can reveal unexpected consequences. We know from our previous work (Rotenberry et al. 2015) that behaving as a satellite can significantly increase male mating success under various ecological and demographic conditions relating to features such as mortality rate, density, and sex ratio. However, throughout the environmental variable space as a whole, increasing satellite behavior has an overall negative effect on male mating success. Moreover, other variables we modeled were generally more important; propensity for satellite behavior has to change greatly to compensate for a much smaller change in, say, the number of females.

Consistent with theory on the evolution of alternative reproductive tactics, changing the risk of parasitism strongly influences the benefits of satellite behavior; as parasitism rate increases, the value of satellite behavior increases, becoming positive at a simulated risk of slightly greater than 0.1 probability of parasitism per night calling. This is approximately the point at which our previous simulations indicated strong selection for a switch in tactics to pure satellite behavior (i.e., behaving as a satellite every night) under many of the conditions we modeled. It is also consistent with the well-established paradigm that the fundamental driver of the caller-satellite tactic in field crickets is fly parasitism (Cade 1975, 1980; Burk 1982; Zuk et al. 1995, 2006; Zuk and Kolluru 1998).

What happens if we remove the opportunity for an alternative mating tactic? We answer this by analyzing the subset of output associated with probability of satellite behavior = 0. Not surprisingly, the negative effect of parasitism increases

Table 2: Standardized path coefficients for total effect (direct + indirect) of each variable on lifetime number of females mated

		Parasitism rate			
	Overall	0	.1	.2	.3
Background mortality	−.31	−.46	−.22	−.18	−.18
Parasitism rate	−.21	...	...	...	...
Satellite behavior	−.09	−.27	−.03	.06	.12
No. males	−.28	−.32	−.36	−.34	−.33
No. females	.42	.43	.56	.57	.56
Phonotaxis probability	.10	.09	.15	.15	.15
Mating probability	.33	.34	.46	.46	.46

Note: Overall = results over all values of variables in table 1 (N = 163,860). Also shown are coefficients for data subset by parasitism rate (N = 40,965 each).

substantially (to −0.41 compared to −0.21 in table 2), while the effect of background mortality decreases somewhat (from −0.31 to −0.26). The number of males becomes slightly more important (−0.31 compared to −0.28) and the number of females slightly less (0.37 compared to 0.42). The effect of phonotaxis is essentially unchanged (0.11 vs. 0.10), and that of mating probability decreases slightly (to 0.29 from 0.33). Thus, the largest effect of introducing satellite behavior is amelioration of parasitism (with concomitant positive effects on life span), but its effects compared to downstream variables remain slight, which suggests that satellite behavior or its equivalent is most likely to evolve and persist when a single selection pressure on signaling is particularly strong.

Unsurprisingly, the largest determinant of male mating success was the number of available females. More females create more opportunities for mating, and variation in female availability appears to be the principal driver of variation in the number of females mated. Female behavior, particularly variation in female choosiness (mating probability on encountering a male), also had a relatively large effect. Here, we modeled choosiness and number of females as independent of each other. However, if choosiness changes with the number of females or with sex ratio, as one might expect (Kokko et al. 2012; Etienne et al. 2014), we could imagine either enhancing or diminishing the effect of large numbers of females by the concomitant effect on how likely they are to mate.

Although modeled as a female trait, mating probability can also be considered a male attribute: on close inspection, some male crickets are simply more attractive to females, perhaps because of attributes of their auditory or olfactory signals (Simmons et al. 2013). Even under high probability of parasitism, where satellite behavior as an alternative tactic has its largest positive effect, the effect associated with female choosiness was almost four times as great (table 2). We interpret this as indicating that sexual selection is likely stronger than natural selection in this model system. Such an asymmetry between natural and sexual selection may explain why ARTs occur when they do; the evolution of satellite behavior, for example, may require circumstances that overcome the inherent disadvantage imposed by reduced female preference.

Similarly, variation in phonotaxis or probability of a female moving toward a male she detects also may be regarded as representing variation in male quality. Its effect size was comparatively low, and that effect changed little with variation in parasitism rate. In essence, we see only a small effect of variation in male calling song attractiveness in our model. Under natural conditions, however, females prefer certain attributes of male calling songs (Simmons et al. 2001; Bailey and Zuk 2008), a trait we thought we had captured by allowing the probability of phonotactic approach to vary from 0.3 to 0.9. The difference likely lies in the spatial component of our simulations; a 20-patch auditory radius means that a calling male can be detected throughout a substantial fraction of the entire 50 × 50-patch landscape, and thus, even a poor-quality male will be exposed to a large fraction of the females available, increasing the odds that at least one will be attracted toward him. The interaction between probability of attraction and the spatial component of detection merits further investigation.

To conclude, although the presence of an alternative mating tactic is enhanced by the introduction of an acoustic parasitoid that greatly increases the cost of calling, other elements of the system, both behavioral and demographic, appear to exert stronger effects on a major measure of male fitness: the lifetime number of females mated. This suggests that an emphasis on when and where alternative tactics are seen will tell only part of the story about the evolution and maintenance of these traits; we require information on some of these other variables that set the context in which tactics are expressed. It is particularly telling that while satellite behavior reduces parasitism and hence allows males to live longer, it is still not as important as other variables such as population density. This limitation suggests that satellite behavior or its equivalent is most likely to evolve and persist when a single selection pressure on signaling is particularly strong and may not be as common under other circumstances. The larger context of demography and ecology may determine more about variation in alternative reproductive behavior and its effect on fitness than has previously been realized.

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